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Establishment, spread, and impact of an invasive planthopper on its invasive host plant: *Prokelisia marginata* (Homoptera: Delphacidae) exploiting *Spartina anglica* (Poales: Poaceae) in Britain

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Abstract. 1. Since its recent arrival in Britain, the planthopper *Prokelisia marginata* has spread widely around saltmarshes on the east and south coast of England and south Wales, feeding on Common Cordgrass, *Spartina anglica*, itself an invasive non-native species.

2. Results suggest that *P. marginata* populations in Britain benefit from a degree of natural enemy release. No evidence of parasitism was found in over 71 000 eggs, nymphs, and adults inspected. The only potential natural enemy control was suggested by a positive correlation between the densities of planthoppers and generalist spiders.

3. Experimental exposure under both glasshouse and field conditions to typical field densities of planthoppers resulted in significant negative effects on a number of host plant performance metrics.

4. *Spartina anglica* is important for stabilising estuarine sediments and has been deliberately planted for this purpose in the past. Its weakening as a result of heavy planthopper herbivory could have serious consequences for the long-term stability of Britain's vulnerable saltmarsh habitats.

Key words. biological invasion, herbivory, natural enemy release, saltmarsh.

Introduction

Invasive alien species are those that establish in areas outside their native range, subsequently spread beyond the location of their introduction, and have an impact on the recipient community (*sensu* Colautti & MacIsaac, 2004). Invasive alien species are the subject of considerable political, public, and academic interest (Huenneke, 1988; IUCN, 2000; Mack *et al.*, 2000) and are considered to be among the top five most severe threats to global biodiversity and ecosystem integrity, along with habitat change, climate change, overexploitation, and pollution (Bellard *et al.*, 2016; IPBES, 2019; Millennium Ecosystem Assessment, 2005; Nelson *et al.*, 2006; Vila *et al.*, 2011; Wagner, 2020). Both the rate and extent of biological invasions continue to escalate (McGeoch *et al.*, 2010), with no indication of levelling off (Seebens *et al.*, 2017). Invasions by new species are therefore altering the structure and composition of often long-established communities (Davis, 2003), with consequent effects on ecological interactions and even the physical and chemical structure of the invaded environments (Ehrenfeld, 2010).

Prokelisia marginata Van Duzee is a stenophagous phloem-feeding planthopper that is native to the Gulf and Atlantic coasts of North America, where it is the most abundant herbivore of the Saltmarsh Cordgrass *Spartina alterniflora* C.E. Hubbard (Denno *et al.*, 1986). Across its entire North American range, the species feeds only on *S. alterniflora*, *S. foliosa* and their hybrids, and the introduced *S. anglica*, avoiding all other sympatrically occurring *Spartina* and other monocotyledonous species (Grevstad *et al.*, 2003). Studies of *P. marginata* in its native range show that it exhibits classic *r*-selected traits, which confer the potential for successful invasion: short generation times and rapid population growth, producing natural densities of up to 1000 adults and 100 000 nymphs per m^2 (Denno *et al.*, 2000; Denno & Grissell, 1979; Gratton & Denno, 2003). Like many planthoppers, *P. marginata* exhibits phenotypic plasticity in wing morphology, with both brachypterous and macropterous forms present in the same population, enabling the planthopper to maximally exploit the prevailing environmental

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conditions (Denno *et al.*, 1986). Macropters are capable of long-distance migration by flight of up to 30 km (Denno *et al.*, 1996), thereby providing them with the strong dispersal capabilities essential for both insects exploiting transient habitats such as saltmarshes and for the expansion of invading populations (Langellotto & Denno, 2001).

The first record of *P. marginata* in Europe was from the Algarve in Portugal in 1994. Later records were reported from Spain in 2008, France in 2009 (Mifsud *et al.*, 2010), the Netherlands (den Bieman & van Klink, 2016), and Norway (Endrestol & Almedal, 2019). *Prokelisia marginata* was first recorded in Britain on Hythe marshes near Southampton in 2008 (Wilson & Muhlerthaler, 2009). A comprehensive invertebrate survey of the same site in 2000 had found no evidence of the planthopper (Kirby, 2000), and although it is possible that it was present in extremely low densities earlier, it is likely that it first arrived in Britain sometime between these dates.

Saltmarshes are of high conservation value, providing a unique habitat for a wide diversity of fauna and flora that are unable to survive elsewhere, as well as an important overwintering refuge for wildfowl (Boorman, 2003; Townend *et al.*, 2011). The presence of hard coastal defences can lead to scouring and erosion on the seaward side while simultaneously preventing natural landward migration of the saltmarsh. In combination with rising sea levels and extreme weather events predicted under global climate change scenarios (Lowe & Meiner, 2012), these factors represent a significant threat to this important habitat and its associated species (Barbier *et al.*, 2011; Finch *et al.*, 2007; Irmler *et al.*, 2002). *Spartina anglica* was first recorded in 1872 in saltmarshes adjacent to Southampton Water and is the fertile allopolyploid of *S. x townsendii*, itself the sterile F_1 hybrid of *S. maritima* and *S. alterniflora* (Gray *et al.*, 1991). Although the parental species still occur in isolated remnant populations, *S. anglica* has become the dominant structuring species in a quarter of Britain's lower saltmarsh communities (Gray *et al.*, 1997). In the past, it was planted specifically to stabilise estuarine sediments, although the resultant monospecific stands hold little value for biodiversity (Bouma *et al.*, 2009; Gan *et al.*, 2009).

Although little studied (Gray *et al.*, 1991), the macroinvertebrate communities of *S. anglica* marshes in Britain appear to be rather sparse; Payne (1973) found only four commonly occurring species in Poole Harbour, three of which appeared to feed on *S. anglica*, although none exclusively. This contrasts markedly with the situation in North America, where *Spartina* marshes are heavily attacked by *P. marginata* and the mirid bug *Trigonotylus uhleri*, both of which are *Spartina* specialists (Denno, 1977; Stiling & Bowdish, 2000; Strong & Stiling, 1983) and reach very high densities (Daehler & Strong, 1995; Denno *et al.*, 1986; Denno *et al.*, 2000). Despite high densities, *P. marginata* apparently has no significant adverse effect on *S. alterniflora* performance and survival, either where both species have co-evolved (Gustafson, Kilheffer, & Silliman, 2006; Roberts & Pullin, 2008) or in invaded ranges where both have coexisted for a substantial period (Daehler & Strong, 1995). However, *S. alterniflora* and *S. anglica* populations that have experienced a lengthy period of separation from *P. marginata*, or have never been in contact, suffer significant deleterious impacts on growth and survival when exposed to the planthopper (Daehler & Strong, 1997; Garcia-Rossi *et al.*, 2003; Wu *et al.*, 1999). In glasshouse trials, previously unexposed *S. anglica* plants suffered 92% mortality after four months of exposure to high densities of *P. marginata*, with surviving plants averaging only 37% of the biomass of control plants (Wu *et al.*, 1999). Field trials of *P. marginata* as a biological control agent of invasive *S. alterniflora* showed an almost 50% reduction in biomass compared to paired controls (Grevstad *et al.*, 2003).

We can assume that British populations of *S. anglica* had no exposure to *P. marginata* prior to its arrival in the early 2000s. Here, we test the impact of *P. marginata* on *S. anglica* in order to determine the susceptibility of the host to the herbivore after a period of separation and the evolution of the plant as a new species. We hypothesise that: (i) *S. anglica* performance measures will be negatively affected by exposure to *P. marginata* feeding and oviposition, and (ii) the strength of this impact will be more severe at greater planthopper densities. We report on the extent of the invaded range of *P. marginata* in Britain and the planthopper's life history, typical population density, and natural enemy complex.

Materials and methods

Field sites

Regular sampling was conducted at two saltmarsh sites dominated by *S. anglica* on the south coast of England: Pagham (50°77′N, 0°78′W) and Hythe (50°86′N, 1°39′W). Data on the geographical distribution of *P. marginata* were collated from records submitted to the UK Auchenorrhyncha Recording Scheme (www.ledra.co.uk) and from invertebrate surveys conducted at *Spartina* sites around the coast of England and Wales.

Prokelisia marginata *demography and invertebrate community sampling*

Samples were taken at both sites on 10 approximately monthly occasions from October 2011 to October 2012. On each occasion, a Vortis suction sampler (Stewart, 2002) was used to take four replicate samples from the vegetation, each consisting of ten 10-second 'sucks' and covering a total sampled area of 1 m^2. *Prokelisia marginata* and all other Hemiptera were identified to the species level, while all other invertebrates were identified to the family level, and counted. In addition, seven *S. anglica* tillers were cut at ground level on each occasion from each site and subsequently searched in the laboratory for the presence of *P. marginata* eggs and egg parasitoids.

Spartina anglica *and* Prokelisia marginata *experimental material*

Spartina anglica plants were grown from rhizome material sampled from Pagham that had been washed, cut to approximately 12 cm lengths including at least one node, and planted in 10 cm (then later transferred to 15 cm) diameter pots containing horticultural-grade silver sand. Pots were watered with fresh

water and kept continually wet but not inundated (following Denno *et al.*, 2000), with the addition of 100% Hoagland nutrient solution (Hoagland & Arnon, 1950) fortnightly. Plants were grown under glasshouse conditions with supplementary lighting (100 W Supanova LED grow lights, 8:2 light ratio comprising 660 nm Red and 430 nm Blue) on an 18:6-hour light: dark cycle.

The allometric relationship between leaf length and biomass in *S. anglica* (Gonzalez Trilla *et al.*, 2013; Nixon & Oviatt, 1973) was calculated using 150 leaves from 20 plants measured to the nearest millimetre from leaf axil to tip and dry weighed to an accuracy of 0.1 mg using a Precisa 125A balance. The linear regression of leaf biomass on leaf length [biomass (g) = 0.0009736*leaf length (mm)] was used to estimate leaf biomass non-destructively in all subsequent experiments.

Prokelisia marginata individuals used in glasshouse experiments were drawn from a breeding culture maintained on clusters of potted *S. anglica* plants grown under glasshouse conditions. The culture was initiated using *S. anglica* plants removed from Hythe showing brown markings indicative of *P. marginata* oviposition (Strong, 1988). New plants were added to the culture as required to maintain a consistent supply of host plant material.

Prokelisia marginata *impact on* Spartina anglica *under glasshouse conditions*

Forty-five potted *S. anglica* plants were placed in individual trays. Individual plants were randomly assigned to one of three treatments: control (no nymphs added), low planthopper density (15 nymphs added), and high planthopper density (30 nymphs added). Five plants of each treatment were randomly assigned to each of three experimental blocks and to a random position within that block in a 3×5 grid configuration. Starting metrics were recorded for each plant: number of leaves, number of tillers, overall plant height, and the length of each leaf (which was then converted to biomass).

Each plant was enclosed by a transparent cylindrical cage constructed from 175 µm polyethylene terephthalate polyester film, 13 cm in diameter, 50 cm tall, and with a nylon gauze lid and a 5×7cm gauze-covered ventilation window positioned 18 cm above the base of the cage. Plants were watered and given nutrients as described above. The experiment ran for 8 weeks, at the end of which the same metrics were recorded for each plant, with additional measurements of fresh and dry weight (to an accuracy of 0.01 g) of total above- and below-ground material.

Prokelisia marginata *impact on* Spartina anglica *under field conditions*

Field cages, 42 cm tall, 31.5 cm in diameter, and enclosing a ground surface area of 780 cm^2, were constructed from inverted white opaque polypropylene buckets with the bases removed and covered with nylon gauze and then secured to the ground with steel tent pegs. Pagham was chosen as the experimental site because background densities of *P. marginata* were very low. Twenty cages were randomly distributed within an area of dense *S. anglica* subject to a moderate but not excessive level of tidal inundation. Cages were randomly assigned to either *Prokelisia* addition or control (no *Prokelisia* added) treatments. Four individual *S. anglica* stems in each cage were designated as 'focal' plants for monitoring. These were loosely tagged with polyvinyl chloride tape, and total leaf length measurements were taken.

Prokelisia marginata were collected the following day from Hythe using the Vortis suction sampler and transported to Pagham. Each *Prokelisia* addition treatment cage received 200 unsexed adults (equivalent to 256 m^{-2}), chosen to reflect the high-density treatment in the glasshouse experiment (224 m^{-2}) and mean natural densities at Hythe the previous June (268 m^{-2}). The experiment ran for 58 days, after which each focal plant was measured for leaf length, and the above-ground parts were removed and subsequently dry-weighed. The remaining standing crop in each cage was also cut at ground level and later dry-weighed. No attempt was made to retain or count any *P. marginata* individuals remaining in the cages.

Statistical analysis

Generalised linear models (GLMs) with a quasi-Poisson error structure (due to overdispersion of residuals) were used to test for correlation between the population density of *P. marginata* and that of other arthropod groups for which at least 200 individuals were collected.

In the glasshouse experiments, differences in plant performance between treatment groups, for continuous response variables, were analysed using linear mixed models (LMMs) with plant change as the response variable, treatment as the explanatory variable, and block as a random factor. Plant change was analysed using relative growth rates (RGRs, i.e. growth during the experimental period divided by the starting measurement) rather than absolute values in order to standardise for unavoidable variation between replicates in the size of plants at the beginning of the experiment. Relative water content was calculated as a percentage of dry biomass. Leaf and tiller count data were analysed using generalised linear mixed-effect models (GLMMs) with a Poisson error structure, log link function, and the Laplace approximation technique (Bolker *et al.*, 2009). As with the LMM structure, plant change was used as the response variable, treatment as the explanatory variable, and block as a random factor.

For the field experiment, all response variables were continuous, normally distributed, and with constant variance. The effect of treatment was analysed using ANOVA, with RGR of focal plants as the response variable and treatment as the explanatory variable. For whole-cage standing crop, the final biomass was used as the response variable.

Analyses were performed with the statistical software R version 3.6.2 (R Core Team, 2019) using the *nlme* (Pinheiro *et al.*, 2012), *lme4* (Bates *et al.*, 2012), and *multcomp* (Hothorn *et al.*, 2008) packages.

Results

Prokelisia marginata *distribution and demography*

Prokelisia marginata has been recorded from 41 10-km squares containing *Spartina* saltmarsh sites from as far north as

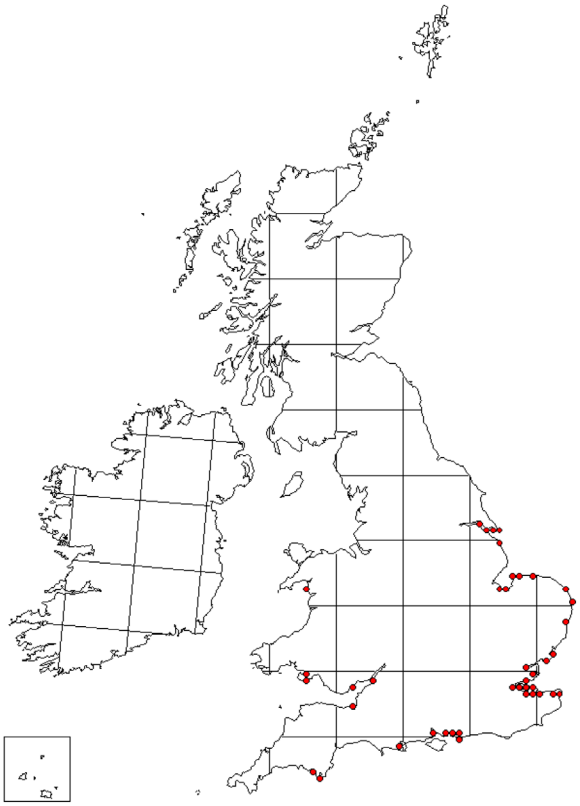

Fig. 1. Distribution of *Prokelisia marginata* in Britain [Colour figure can be viewed at wileyonlinelibrary.com].

the Humber estuary and as far west as the Gower Peninsular in Wales (Fig. 1). All sites containing *S. anglica* and specifically searched for *P. marginata* revealed the planthopper to be present, although densities varied considerably. Seasonal changes in *P. marginata* density at Hythe revealed a bivoltine life cycle, the second generation being considerably larger than the first, reaching a peak in August with densities of 1252 adults per m^2 (Fig. 2). The seasonal patterns for eggs and nymphs were similar, with peaks occurring one and two months later, respectively. Densities at Pagham were substantially lower than at Hythe throughout the sampling period. The percentage of macropterous adults at Hythe was 71% in May, reaching a peak of 99% in July and falling no lower than 96% for the rest of the season.

Invertebrate community composition

Densities of all other arthropod groups were lower than *P. marginata* by at least one, and more frequently two, order of magnitude (Table S1). The density of *P. marginata* was positively correlated with the density of spiders (both sites: $F = 52.97$, $P < 0.001$; Hythe only: $F = 10.24$, $P = 0.002$; Pagham only: $\chi^2 = 4.47$, $P = 0.03$; Figs 3 and 4). The density of spiders was not correlated with that of any other potential prey group: Hemiptera (excluding *P. marginata*), Collembola, Coleoptera, or Diptera. Over 71 000 *P. marginata* eggs, nymphs, and adults collected over the course of 13 months were examined for the presence of parasitoids, but none were found.

Effect of Prokelisia marginata *on* Spartina anglica *performance*

Exposure to *P. marginata* under glasshouse conditions had significant negative effects on *S. anglica* relative growth rates in overall height; above-ground and root biomass; and in the number of new tillers gained at high, but not at low, planthopper density. The number of new leaves gained and the relative water content of shoot material were negatively affected in both the low- and the high-density treatments. There was no effect of either treatment level on the root: shoot ratio of plants (Table 1). Exposure to *P. marginata* under semi-natural field conditions had significant negative impacts on relative leaf length gain of focal *S. anglica* plants and on final whole-cage biomass (Table 2; Fig. 5).

Discussion

The invasion status of Prokelisia marginata *in Britain*

Our results show *P. marginata* to be in the successful early stages of invasion in Britain, having reached densities matching those reported from its native range in North America (Denno & Peterson, 2000) and outnumbering other arthropod groups by at least one, frequently two, order of magnitude. The pathway by which *P. marginata* arrived in Britain is unknown, although the most likely is via transport of eggs laid inside plant material. On the assumption that *P. marginata* first arrived in Britain sometime after 2000, however, its colonisation of saltmarshes around the coasts of England and Wales has been exceptionally rapid. Further northward range expansion, at least on the east coast, may be curtailed by the distribution of the host plant (Preston *et al.*, 2002).

Prokelisia marginata exhibits functional traits that promote its success as an invasive alien species (Denno *et al.*, 1985). It appears to be bivoltine in Britain, compared to trivoltine in its native range on the Atlantic coast of North America (Denno & Roderick, 1990), as a consequence of the difference in latitude between the study sites (51°N and 39°N, respectively). Despite this difference in voltinism, however, peak adult population densities at one of the British sites were similar to those recorded in the native range (Denno *et al.*, 2000). Growth rates that allow populations to reach such high densities in a single season, together with wing polymorphism enabling rapid dispersal in response to crowding, substantially explain the invasion success of this species. In addition, the relatively unsaturated nature of invertebrate communities in British saltmarshes (Ford *et al.*, 2013), especially the sap-feeding guild, means they are particularly prone to invasion and numerical domination by *P. marginata*.

In Britain, *P. marginata* currently appears to benefit from an absence of specialist natural enemies. In its native range, *P. marginata* can suffer heavily from a parasitoid attack: up to 40% of nymphs and adults by Strepsiptera (Stiling *et al.*, 1991) and 27–100% of eggs by Mymaridae (Stiling

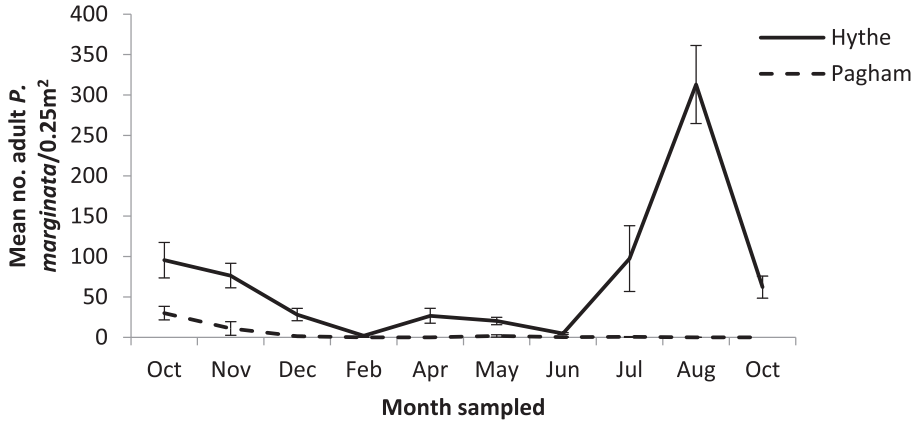

Fig. 2. Mean number (±1 SEM) of adult *Prokelisia marginata* per 0.25 m^2 between October 2011 and October 2012 at Hythe and Pagham.

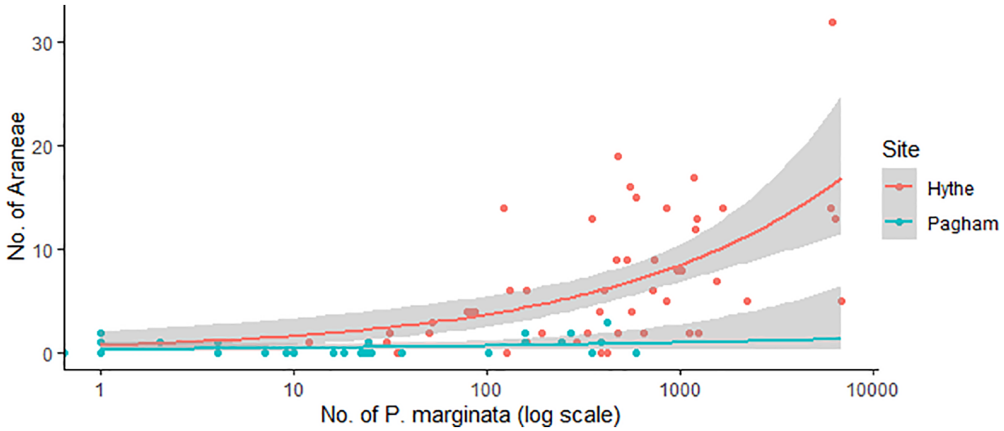

Fig. 3. Relationship between number of *Prokelisia marginata* (note log scale) and Araneae per 0.25 m^2 quadrat sample at Hythe and Pagham. Fitted lines predicted from the generalised linear model with 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com].

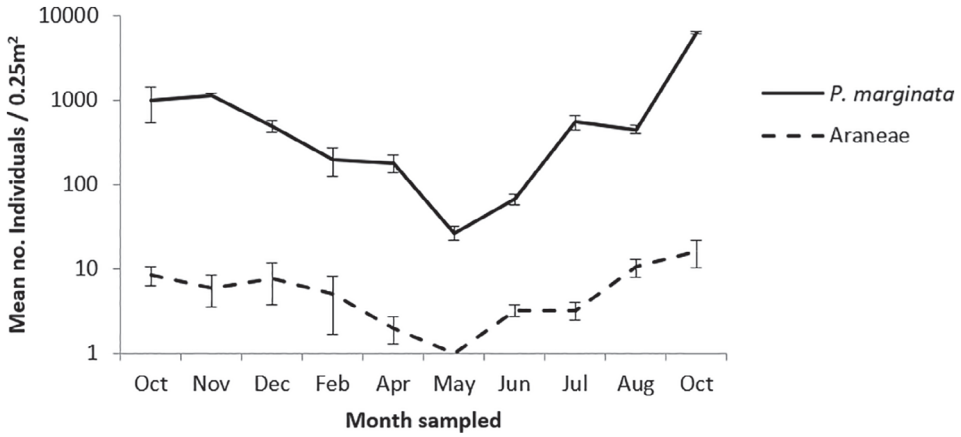

Fig. 4. Mean number (±1 SEM; log scale) of *Prokelisia marginata* (adults and nymphs) and Araneae at Hythe per 0.25 m^2. Sampling dates as in Fig. 2.

Table 1. Effect of *Prokelisia marginata* on *Spartina anglica* performance.

	d.f.	Control mean (SEM)	Treatment mean (SEM)	*L* ratio	χ^2	*P*
Biomass relative gain						
Treatment (whole model)	40	2.42 (0.63)	1.70 (0.29)	15.58		<0.001***
Low density (*post-hoc*)			2.04 (0.47)			0.271
High density (*post-hoc*)			1.36 (0.32)			<0.001***
No. new tillers gained						
Treatment (whole model)	40	2.07 (0.43)	1.17 (0.24)		6.65	0.036*
Low density (*post-hoc*)			1.40 (0.40)			0.394
High density (*post-hoc*)			0.93 (0.25)			0.037*
No. new leaves gained						
Treatment (whole model)	40	15.87 (1.45)	11.50 (0.80)		15.09	<0.001***
Low density (*post-hoc*)			12.07 (1.32)			0.015*
High density (*post-hoc*)			10.93 (0.94)			<0.001***
Relative water content						
Treatment (whole model)	40	2.17 (0.18)	1.68 (0.14)	17.56		<0.001***
Low density (*post-hoc*)			1.69 (0.15)			<0.001***
High density (*post-hoc*)			1.67 (0.23)			<0.001***
Final root biomass (g)						
Treatment (whole model)	40	8.42 (0.65)	6.85 (0.72)	6.42		0.040*
Low density (*post-hoc*)			8.14 (0.91)			0.988
High density (*post-hoc*)			5.56 (1.03)			0.042*
Root: shoot ratio						
Treatment (whole model)	40	1.44 (0.11)	1.54 (0.13)	3.39		0.184
Low density (*post-hoc*)			1.74 (0.18)			0.363
High density (*post-hoc*)			1.34 (0.18)			0.916
Relative height gain						
Treatment (whole model)	40	0.49 (0.08)	0.26 (0.04)	13.11		0.001***
Low density (*post-hoc*)			0.31 (0.07)			0.057
High density (*post-hoc*)			0.22 (0.05)			<0.001***

Individual treatment levels refer to low *P. marginata* density (15 individuals added) and high *P. marginata* density (30 individuals added) treatments. Whole-model analyses refer to comparisons with control (no *P. marginata* added) replicates. Post-hoc test refers to Tukey HSD using 95% CI. Test statistics are log-likelihood (*L*) ratio for LMMs and $\chi 2$ for GLMMs. Relative metrics indicate ratios of post- to pre-experiment measurements. Significance levels indicated by: *≤0.05; **≤0.01;***≤0.001.

Table 2. Effect of *Prokelisia marginata* on *Spartina anglica* performance measures in field conditions.

	d.f.	Control mean (SEM)	Treatment mean (SEM)	*F*	*P*
Relative leaf length gain					
Treatment	1	1.14 (0.08)	0.84 (0.05)	4.88	0.040*
Residuals	18				
Final whole-cage biomass (g)					
Treatment	1	83.69 (5.23)	60.42 (4.22)	5.99	0.025*
Residuals	18				

Treatments are control (no *P. marginata*) and *Prokelisia* (200 individuals added). Relative metrics indicate ratios of post- to pre-experiment measurements. Significance levels indicated by: *≤0.05.

& Strong, 1982); the latter appear to drive host population cycles (Reeve *et al.*, 1994). The lack of parasitoids of any life history stages in British populations of *P. marginata* fits with the general pattern that parasitoid attack rates tend to be much lower on hosts in their invaded, compared to their native, ranges (Cornell & Hawkins, 1993). For example, parasitism rates in the leaf-mining moth *Cameraria ohridella*, even of generalist parasitoids, were very low in areas that it had recently invaded but increased as a function of residence time (Grabenweger *et al.*, 2010).

Generalist predators may exert the greatest numerical control on *P. marginata* populations. Spiders have been identified as the primary natural enemies of both adult and nymphal *P. marginata* in their native range (Denno *et al.*, 2002; Gratton & Denno, 2005). *Prokelisia marginata* appears to be more susceptible to predation than co-occurring prey such as leafhoppers and mirid bugs due to its ineffective predator avoidance behaviour (Dobel & Denno, 1994) and typical adoption of a low position within the *Spartina* canopy (Vince *et al.* 1981). The high densities of *P. marginata* at Hythe appear to have elicited a strong numerical response in spiders, although this may still currently be insufficient to regulate planthopper population growth.

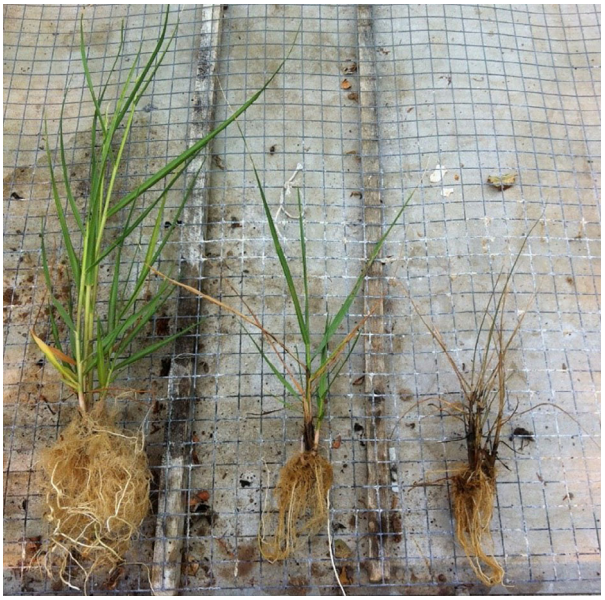

Fig. 5. A selection of *Spartina anglica* plants at the end of the experimental period illustrating the negative effects of *Prokelisia marginata* exposure on plant growth. Treatments (left to right): control (no. *P. marginata*); low density (15 *P. marginata* individuals added); high density (30 *P. marginata* individuals added). [Colour figure can be viewed at wileyonlinelibrary.com].

Impact of Prokelisia marginata *on* Spartina anglica *performance metrics*

Exposure to *P. marginata* herbivory and oviposition had a significant negative impact on all the *S. anglica* functional traits examined under glasshouse conditions. As predicted, impacts were more severe in high-density treatments, although it should be noted that crowding levels in this treatment were still somewhat lower than the mean densities recorded at one of the field sites. Plants in this treatment had greatly reduced height and root biomass, indicative of reduced competitive ability, while the reduced number and total length of leaves would have had an impact on photosynthetic potential (Olmstead *et al.*, 1997; Strong *et al.*, 1984). The reduction of relative water content found in plants subject to both treatment levels would have had the potential to restrict transpiration and nutrient uptake, reduce photosynthetic efficiency, and ultimately limit productivity (Zhang *et al.*, 2012). Similar impacts of exposure to *P. marginata* were apparent under field conditions.

Prokelisia marginata are stenophagous on only a small range of *Spartina* species (Grevstad *et al.*, 2003). As all other *Spartina* species in Britain are rare and extremely localised (Lacambra *et al.*, 2004), *S. anglica* provides the main mechanism for the further establishment and spread of *P. marginata*. Our study is the first to examine the interaction between *P. marginata* and *S. anglica* outside North America, where the herbivore showed early promise as a potential biological control agent of the grass (Grevstad *et al.*, 2003). Our findings lend weight to the conclusions of North American studies that long-separated and previously unexposed *Spartina* populations are vulnerable to attack by *P. marginata* in a way that co-evolved and coexisting plants are not (Daehler & Strong, 1995; Grevstad *et al.*, 2003; Wu *et al.*, 1999).

British populations of *S. anglica* have so far benefitted from a degree of natural enemy escape (Gray *et al.*, 1991), in contrast to North American *S. alterniflora* marshes, which hold a diverse assemblage of host-specific herbivores (Gratton & Denno, 2005). There are no native specialist *Spartina* herbivores in any part of Europe (Garcia-Rossi *et al.*, 2003). Daehler and Strong (1995) found that the top–down effects of insect herbivores on *S. alterniflora* in San Francisco Bay were minimal and suggested that this may be because few other stressors have a major impact on the plant, which occurs in large, monospecific stands and is subject to little or no interspecific competition (Strong & Ayres, 2013). Dense, monospecific stands are less frequent in Britain, however, where *S. anglica* is usually present in more mixed communities with other halophytes (Boorman, 2003; Dargie, 2000; Gray *et al.*, 1991; Huckle *et al.*, 2004). *S. anglica* in Britain may consequently be subject to greater competition-induced stress, already noted as a potential contributing factor to the die-back recorded in recent decades (Lacambra *et al.*, 2004), and may thus be inherently more vulnerable to the deleterious impacts of a novel and abundant insect herbivore.

Prokelisia marginata is still in the relatively early stages of invasion in the United Kingdom. Already, however, it appears to have spread rapidly from its probable site of entry and has reached densities in some populations that, as we have shown under field conditions, will have significant deleterious impacts on the host plant. Invasion lag and other complexities of the invasion process mean that the full effects of an invader may not be seen until a considerable time has elapsed after its arrival (Strayer *et al.*, 2006). Studies have found herbivory by a range of invertebrates to be a significant driver of *Spartina* sp. die-back (Bertness *et al.*, 2014; Hughes & Paramor, 2004; Jefferies *et al.*, 2006; Silliman & Zieman, 2001), with a resulting reduction in the sediment retention abilities of the grass (Gleason *et al.*, 1979). In addition, herbivory has been shown to interact with other biological and physical stressors to impact saltmarsh plant productivity and community composition (Alberti *et al.*, 2008; Jimenez *et al.*, 2012; Li & Pennings, 2017; Montemayor *et al.*, 2020). Further investigation is needed to assess whether continued *P. marginata* population growth and spread may act additively, or even synergistically, with other biotic and abiotic factors to restrain or inhibit growth in British *Spartina* species or increase the rate of die-back. A reduction in plant vigour, such as has been seen in *S. anglica* die-back in southern England, may have a deleterious impact on its ability to dissipate wave action and currents across affected saltmarshes (Adnitt *et al.*, 2007), consequently reducing the extent to which it helps to reduce coastal flooding. While the role of *S. anglica* in stabilising estuarine sediments remains complex, and in some cases contentious, early indications suggest that *P. marginata* has the potential to contribute to a significant change in the composition of British saltmarsh plant communities over the coming decades. Further research is needed to clarify the nature and extent of these potential impacts on this important and already heavily challenged habitat.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Number of individuals of classified invertebrate groups collected at the Hythe and Pagham field sites between October 2011 and October 2012.

References

Adnitt, C., Brew, D., Cottle, R., Hardwick, M., John, S., Leggett, D. *et al.* (2007) *Joint Defra/Environment Agency Flood and Coastal Erosion Risk Management R&D Programme: Saltmarsh Management Manual*. Environment Agency, Bristol.

Alberti, J., Escapa, M., Iribarne, O., Silliman, B.R. & Bertness, M. (2008) Crab herbivory regulates plant facilitative and competitive processes in Argentinean marshes. *Ecology*, **89**, 155–164.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. & Silliman, B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs*, **81**, 169–193.

Bates, D., Maechler, M. & Bolker, B. 2012. *lme4: Linear Mixed-Effects Models Using S4 Classes*. URL http://CRAN.R-project.org/package=lme4.

Bellard, C., Cassey, P. & Blackburn, T.M. (2016) Alien species as a driver of recent extinctions. *Biology Letters*, **12**, 20150623.

Bertness, M.D., Brisson, C.P., Bevil, M.C. & Crotty, S.M. (2014) Herbivory drives the spread of salt marsh die-off. *PLoS One*, **9**, e92916.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. *et al.* (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Boorman, L. A. 2003. Saltmarsh Review. An Overview of Coastal Saltmarshes, Their Dynamic and Sensitivity Characteristics for Conservation and Management. JNCC Report no. 334. (ed. JNCC). JNCC, Peterborough.

Bouma, T.J., Ortells, V. & Ysebaert, T. (2009) Comparing biodiversity effects among ecosystem engineers of contrasting strength: macrofauna diversity in *Zostera noltii* and *Spartina anglica* vegetations. *Helgoland Marine Research*, **63**, 3–18.

Colautti, R.I. & MacIsaac, H.J. (2004) A neutral terminology to define 'invasive' species. *Diversity and Distributions*, **10**, 135–141.

Cornell, H.V. & Hawkins, B.A. (1993) Accumulation of native parasitoid species on introduced herbivores – a comparison of hosts and native and hosts as invaders. *American Naturalist*, **141**, 847–865.

Daehler, C.C. & Strong, D.R. (1995) Impact of high herbivore densities on introduced smooth cordgrass, *Spartina alterniflora*, invading San Francisco Bay, California. *Estuaries*, **18**, 409–417.

Daehler, C.C. & Strong, D.R. (1997) Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia*, **110**, 99–108.

Dargie, T. 2000. NVC Survey of Saltmarsh and Other Habitat in the Dee and Clwyd Estuaries. Report to Countryside Council for Wales and English Nature. London.

Davis, M.A. (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience*, **53**, 481–489.

den Bieman, C.F.M. & van Klink, R. (2016) De slijkgrascicade *Prokelisia marginata*: een Amerikaanse spoorcicade in Nederland (Homoptera: Auchenorrhyncha: Delphacidae). *Entomologische Berichten*, **76**, 218–225.

Denno, R.F. (1977) Comparison of assemblages of sap-feeding insects (Homoptera-Hemiptera) inhabiting two structurally different salt marsh grasses in genus Spartina. *Environmental Entomology*, **6**, 359–372.

Denno, R.F., Douglass, L.W. & Jacobs, D. (1985) Crowding and host plant nutrition–environmental determinants of wing-form in *Prokelisia marginata*. *Ecology*, **66**, 1588–1596.

Denno, R.F., Douglass, L.W. & Jacobs, D. (1986) Effects of crowding and host plant nutrition on a wing-dimorphic planthopper. *Ecology*, **67**, 116–123.

Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L. & Huberty, A.F. (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology*, **83**, 1443–1458.

Denno, R.F. & Grissell, E.E. (1979) Adaptiveness of wing-dimorphism in the salt marsh-inhabiting planthopper *Prokelisia marginata* (Homoptera, Delphacidae). *Ecology*, **60**, 221–236.

Denno, R.F. & Peterson, M.A. (2000) Caught between the devil and the deep blue sea, mobile planthoppers elude natural enemies and deteriorating host plants. *American Entomologist*, **46**, 95–109.

Denno, R.F., Peterson, M.A., Gratton, C., Cheng, J.A., Langellotto, G.A., Huberty, A.F. *et al.* (2000) Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology*, **81**, 1814–1827.

Denno, R.F. & Roderick, G.K. (1990) Population biology of planthoppers. *Annual Review of Entomology*, **35**, 489–520.

Denno, R.F., Roderick, G.K., Peterson, M.A., Huberty, A.F., Dobel, H.G., Eubanks, M.D. *et al.* (1996) Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecological Monographs*, **66**, 389–408.

Dobel, H.G. & Denno, R.F. (1994) *Predator: Planthopper Interactions. Pages 325–399 Planthoppers: Their Ecology and Management*. Chapman & Hall, London.

Ehrenfeld, J.G. (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 59–80.

Endrestol, A. & Almedal, S. (2019) *Prokelisia marginata* (Van Duzee, 1897) (Hemiptera, Delphacidae) recorded for the first time in Northern Europe. *Norwegian Journal of Entomology*, **66**, 33–38.

Finch, O.-D., Krummen, H., Plaisier, F. & Schultz, W. (2007) Zonation of spiders (Araneae) and carabid beetles (Coleoptera: Carabidae) in Island salt marshes at the North Sea coast. *Wetlands Ecology and Management*, **15**, 207–228.

Ford, H., Garbutt, A., Jones, L. & Jones, D.L. (2013) Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance

and functional group structure. *Insect Conservation and Diversity*, **6**, 189–200.

Gan, X.J., Cai, Y.T., Choi, C.Y., Ma, Z.J., Chen, J.K. & Li, B. (2009) Potential impacts of invasive *Spartina alterniflora* on spring bird communities at Chongming Dongtan, a Chinese wetland of international importance. *Estuarine Coastal and Shelf Science*, **83**, 211–218.

Garcia-Rossi, D., Rank, N. & Strong, D.R. (2003) Potential for self-defeating biological control? Variation in herbivore vulnerability among invasive *Spartina* genotypes. *Ecological Applications*, **13**, 1640–1649.

Gleason, M.L., Elmer, D.A., Pien, N.C. & Fisher, J.S. (1979) Effects of stem density upon sediment retention by saltmarsh cord grass, *Spartina alterniflora* Loisel. *Estuaries*, **2**, 271–273.

Gonzalez Trilla, G., Marta Borro, M., Soledad Morandeira, N., Schivo, F., Kandus, P. & Marcovecchio, J. (2013) Allometric scaling of dry weight and leaf area for *Spartina densiflora* and *Spartina alterniflora* in two Southwest Atlantic saltmarshes. *Journal of Coastal Research*, **29**, 1373–1381.

Grabenweger, G., Kehrli, P., Zweimueller, I., Augustin, S., Avtzis, N., Bacher, S., Freise, J., Girardoz, S., Guichard, S., Heitland, W., Lethmayer, C., Stolz, M., Tomov, R., Volter, L. & Kenisa, M. (2010) Temporal and spatial variations in the parasitoid complex of the horse chestnut leafminer during its invasion of Europe. *Biological Invasions*, **12**, 2797–2813.

Gratton, C. & Denno, R.F. (2003) Inter-year carryover effects of a nutrient pulse on Spartina plants, herbivores, and natural enemies. *Ecology*, **84**, 2692–2707.

Gratton, C. & Denno, R.F. (2005) Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. *Restoration Ecology*, **13**, 358–372.

Gray, A.J., Marshall, D.F. & Raybould, A.F. (1991) A century of evolution in *Spartina anglica*. *Advances in Ecological Research*, **21**, 1–62.

Gray, A. J., A. F. Raybould, and S. L. Brown. 1997. The Environmental Impact of *Spartina anglica*: Past, Present and Predicted. *Proceedings of the Second International Spartina Conference*, pp. Pages 39–45. Olympia, WA.

Grevstad, F.S., Strong, D.R., Garcia-Rossi, D., Switzer, R.W. & Wecker, M.S. (2003) Biological control of *Spartina alterniflora* in Willapa Bay, Washington using the planthopper *Prokelisia marginata*: agent specificity and early results. *Biological Control*, **27**, 32–42.

Gustafson, D.J., Kilheffer, J. & Silliman, B.R. (2006) Relative effects of *Littoraria irrorata* and *Prokelisia marginata* on *Spartina alterniflora*. *Estuaries and Coasts*, **29**, 639–644.

Hoagland, D.R. & Arnon, D.I. (1950) The water culture method for growing plants without soil. *California Agricultural Experiment Station Circular*, **347**, 1–32.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.

Huckle, J.M., Marrs, R.H. & Potter, J.A. (2004) Spatial and temporal changes in salt marsh distribution in the Dee estuary, NW England, determined from aerial photographs. *Wetlands Ecology and Management*, **12**, 483–498.

Huenneke, L. (1988) SCOPE program on biological invasions: a status report. *Conservation Biology*, **2**, 8–14.

Hughes, R.G. & Paramor, O.A.L. (2004) On the loss of saltmarshes in south-East England and methods for their restoration. *Journal of Applied Ecology*, **41**, 440–448.

IPBES (2019) *Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES secretariat, Bonn, Germany.

Irmler, U., Heller, K., Meyer, H. & Reinke, H.D. (2002) Zonation of ground beetles (Coleoptera: Carabidae) and spiders (Araneida) in salt marshes at the North and the Baltic Sea and the impact of the predicted sea level increase. *Biodiversity and Conservation*, **11**, 1129–1147.

IUCN. 2000. IUCN Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species. *Fifth Meeting of the Conference of the Parties to the Convention on Biological Diversity*. IUCN, Nairobi, Kenya.

Jefferies, R.L., Jano, A.P. & Abraham, K.F. (2006) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, **94**, 234–242.

Jimenez, J.M., Wieski, K., Marczak, L.B., Ho, C.-K. & Pennings, S.C. (2012) Effects of an omnivorous katydid, salinity, and nutrients on a planthopper-*Spartina* food web. *Estuaries and Coasts*, **35**, 475–485.

Kirby, P. (2000) *Hythe Marshes Invertebrate Survey 2000: Report to Hampshire County Council*. Jonathan Cox Associates, Hampshire.

Lacambra, C., Cutts, N., Allen, J., Burd, F. & Elliott, M. (2004) *English Nature Research Reports No. 527 Spartina anglica: A Review of Its Status, Dynamics and Management*. English Nature, Peterborough.

Langellotto, G.A. & Denno, R.F. (2001) Benefits of dispersal in patchy environments: mate location by males of a wing-dimorphic insect. *Ecology*, **82**, 1870–1878.

Li, S.Z. & Pennings, S.C. (2017) Timing of disturbance affects biomass and flowering of a saltmarsh plant and attack by stem-boring herbivores. *Ecosphere*, **8**, https://doi.org/10.1002/ecs2.1675.

Lowe, J. & Meiner, A. (2012) Coastal Zones. *Climate Change, Impacts and Vulnerability in Europe 2012: An Indicator-Based Report*. European Environment Agency, Copenhagen.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.

McGeoch, M.A., Butchart, S.H.M., Spear, D., Marais, E., Kleynhans, E.J., Symes, A. *et al.* (2010) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, **16**, 95–108.

Mifsud, D., Cocquempot, C., Muehlethaler, R., Wilson, M. & Streito, J.-C. (2010) Other Hemiptera Sternorrhyncha (Aleyrodidae, Phylloxeroidea, and Psylloidea) and Hemiptera Auchenorrhyncha. Chapter 9.4. *BioRisk*, **4**, 511–552.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Wellbeing: Biodiversity Synthesis*. World Resources Institute, Washington DC.

Montemayor, D.I., Sparks, E.L. & Cebrian, J. (2020) Herbivory patterns along the intertidal gradient of *Juncus roemerianus* salt marshes. *Marine Environmental Research*, **153**, 104814.

Nelson, G.C., Bennett, E., Berhe, A.A., Cassman, K., DeFries, R., Dietz, T. *et al.* (2006) Anthropogenic drivers of ecosystem change: an overview. *Ecology and Society*, **11**, www.jstor.org/stable/26266018.

Nixon, S.W. & Oviatt, C.A. (1973) Analysis of local variation in the standing crop of *Spartina alterniflora*. *Botanica Marina*, **16**, 103–109.

Olmstead, K.L., Denno, R.F., Morton, T.C. & Romeo, J.T. (1997) Influence of *Prokelisia* planthoppers on amino acid composition and growth of *Spartina alterniflora*. *Journal of Chemical Ecology*, **23**, 303–321.

Payne, K. (1973) A survey of the *Spartina*-feeding insects in Pool harbour, Dorset. *Entomologist's Monthly Magazine*, **108**, 66–79.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarker, and R Development Core Team. 2012. nlme: Linear and Nonlinear Mixed Effects Models. URL http://CRAN.R-project.org/web/packages/nlme/citation.html.

Preston, C.D., Pearman, D.A. & Dines, T.D. (2002) *New Atlas of the British and Irish Flora*. Oxford University Press, Oxford.

R Core Team (2019) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reeve, J.D., Cronin, J.T. & Strong, D.R. (1994) Parasitism and generation cycles in a saltmarsh planthopper. *Journal of Animal Ecology*, **63**, 912–920.

Roberts, P.D. & Pullin, A.S. (2008) The effectiveness of management interventions for the control of *Spartina* species: a systematic review and meta-analysis. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **18**, 592–618.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M. *et al.* (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications*, **8**, https://doi.org/10.1038/ncomms14435.

Silliman, B.R. & Zieman, J.C. (2001) Top-down control of *Spartina alterniflora* production by periwinkle grazing in a *Virginia saltmarsh*. *Ecology*, **82**, 2830–2845.

Stewart, A.J.A. (2002) Techniques for sampling Auchenorrhyncha in grasslands. *Denisia*, **4**, 491–512.

Stiling, P. & Bowdish, T.I. (2000) Direct and indirect effects of plant clone and local environment on herbivore abundance. *Ecology*, **81**, 281–285.

Stiling, P., Throckmorton, A., Silvanima, J. & Strong, D. (1991) Biology of and rates of parasitism by nymphal and adult parasites of the salt marsh-inhabiting planthoppers *Prokelisia marginata* and *P. dolus*. *Florida Entomologist*, **74**, 81–87.

Stiling, P.D. & Strong, D.R. (1982) Egg density and the intensity of parasitism in *Prokelisia marginata* (Homoptera, Delphacidae). *Ecology*, **63**, 1630–1635.

Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, **21**, 645–651.

Strong, D.R. (1988) A mite, *Ogmotarsonemus erepsis* (Tarsonemiae), in oviposition incisions of the planthopper *Prokelisia marginata* (Homoptera, Delphacidae) on the saltmarsh cordgrass *Spartina alterniflora*. *Florida Entomologist*, **71**, 387–389.

Strong, D.R. & Ayres, D.R. (2013) Ecological and evolutionary misadventures of *Spartina*. *Annual Review of Ecology, Evolution and Systematics*, **44**, 389–410.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984) *Insects on Plants: Community Patterns and Mechanisms*. London, Blackwell.

Strong, D.R. & Stiling, P.D. (1983) Wing dimorphism changed by experimental density manipulation in a planthopper (*Prokelisia marginata*, Homoptera, Delphacidae). *Ecology*, **64**, 206–209.

Townend, I., Fletcher, C., Knappen, M. & Rossington, K. (2011) A review of salt marsh dynamics. *Water and Environment Journal*, **25**, 477–488.

Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, V., Maron, J.L. *et al.* (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702–708.

Vince, S.W., Valiela, I. & Teal, J.M. (1981) An experimental study of the structure of herbivorous insect communities in a saltmarsh. *Ecology*, **62**, 1662–1678.

Wagner, D.L. (2020) Insect declines in the Anthropocene. *Annual Review of Entomology*, **65**, 457–480.

Wilson, M. & Muhlerthaler, R. (2009) Hemiptera report. *British Journal of Entomology and Natural History*, **22**, 185.

Wu, M.Y., Hacker, S., Ayres, D. & Strong, D.R. (1999) Potential of *Prokelisia* spp. as biological control agents of English cordgrass, *Spartina anglica*. *Biological Control*, **16**, 267–273.

Zhang, Q., Li, Q. & Zhang, G. (2012) Rapid determination of leaf water content using VIS/NIR spectroscopy analysis with wavelength selection. *Spectroscopy-An International Journal*, **27**, 93–105.

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